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Research

Density dependence and spatial heterogeneity limit the population growth rate of invasive pines at the landscape scale

Rowan Sprague, Philip E. Hulme, Elena Moltchanova and William Godsoe

R. Sprague (https://orcid.org/0000-0002-6044-1006) ✉ (rowan.sprague@gmail.com), P. E. Hulme and W. Godsoe, Bio-Protection Research Centre, Lincoln Univ., Canterbury, New Zealand. – E. Moltchanova, School of Mathematics and Statistics, Univ. of Canterbury, New Zealand.

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Determining population growth across large scales is difficult because it is often impractical to collect data at large scales and over long timespans. Instead, the growth of a population is often only measured at a small, plot-level scale and then extrapolated to derive a mean field estimate. However, this approach is prone to error since it simplifies spatial processes such as the neighbourhood effects of density and dispersal. We present a novel approach that estimates how spatial processes derived from the effects of density and dispersal affect population growth between plot scales and landscape scales. The method is based on a scale transition theory and calculates a transition term to measure the spatial scaling of population growth, which we extend to unstable, expanding populations in order to assess whether landscape-scale population dynamics are different from those estimated at smaller spatial scales. We illustrate this approach using aerial imagery of eight locations in New Zealand experiencing non-native pine invasions. Analyses examined the dynamics at a plot scale (1 ha) and compared this to estimates across entire landscapes (between 24 and 1600 ha), in several cases for more than one time period. We used a Bayesian spatial random effects model to examine population growth and to account for neighbourhood effects and dispersal between plots in a rapidly changing system.

We found that the estimates of the scale transition term were typically 10–25% of the mean field estimates, which led to mean field estimates of population growth extrapolated from plots being considerably higher than landscape estimates. The approach we have developed will not only have applications for predicting the populations' growth of invasive species, but also for studies examining the scaling of landscape-scale phenomena.

Keywords: dispersal, invasion ecology, landscape demography, *Pinus*, population growth, scale-dependence

Introduction

Ecologists need reliable methods to scale up population dynamics from plots to landscapes (Scholes 2017). A qualitative understanding of this issue is vital for determining the large-scale effects of species interactions, climate change and population persistence (Clark et al. 2011, Early et al. 2016, Godsoe et al. 2017, Usinowicz and Levine

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2018). However, most studies attempting to address large-scale ecological process are only undertaken at a plot-level scale (Salguero-Gómez et al. 2015, Gurevitch et al. 2016, Treurnicht et al. 2016, Estes et al. 2018). Estimates of population growth will differ between plot and landscape scales because of spatially scale-dependent processes shaped by environmental heterogeneity and natural variations in population density (Levin 1992, Steen and Haydon 2000, Freckleton and Watkinson 2002, Sandel 2015). Density dependent growth is particularly important for plants because they cannot move to change their local neighbourhood density (Stoll and Weiner 2000, Peters 2003, Law et al. 2009). The spatial variability of local density dependence can affect population dynamics at larger spatial scales, but it is difficult to capture this effect when observing processes at a small scale (Wisz et al. 2013, Belmaker et al. 2015, Sandel 2015).

In practice, the most common approach is to ignore scale dependent processes by averaging population dynamics over a landscape. When we do so, we revert to what is known as the mean field approximation of population growth (Melbourne and Chesson 2005). The mean field is calculated by averaging density and therefore averaging the density-dependent effects on population growth (Dieckmann et al. 2000, Morozov and Poggiale 2012).

However, the mean field approximation is flawed. This estimate is accurate only when density and individual growth responses to density are uniform across a landscape. Since the density of individuals varies across a landscape (Turner and Gardner 2015), we cannot assume that every individual has the same local neighbourhood density and therefore experiences the same growth across a landscape in response to its neighbourhood effects (Murrell et al. 2001, Ying et al. 2014). In fact, many studies (Stoll and Weiner 2000, Zenner and Peck 2018) have not found support for the mean field approximation of population growth.

One way to better estimate broad scale population growth is to explicitly model population growth in each individual habitat patch. This approach is data intensive and provides limited insights about the circumstances where population growth deviates from the mean field approximation. As an alternative, some have advocated using a scale transition approach to scale up population growth (Chesson et al. 2005, Chesson 2012, Godsoe et al. 2017, Usinowicz and Levine 2018). In scale transition theory (Chesson et al. 2005), a scale transition term accounts for the scaling of population growth between a small scale (i.e. less than one hectare) and a landscape scale (several km^2). This approach approximates the difference between local and landscape population growth rates using information on variation in density among plots and density dependence of population growth within plots (Chesson et al. 2005, Melbourne et al. 2005). In doing so, a scale transition term quantifies the effect of spatial processes on population growth, represented by the difference between the mean field approximation and the landscape estimate of population growth (Melbourne and Chesson 2006). Because this method focuses on population dynamics at the plot level, it requires far less data than other scaling approaches such as spatial moment dynamics (Adams et al. 2013, Cipriotti et al. 2016). A disadvantage of the scale transition theory is that we cannot tease apart interactions between mechanisms which shape population growth because it does not gather data on individuals nor capture complete life histories (Law et al. 2003). However, this simplification makes the methodology less computationally demanding and estimating the scale transition term is straightforward. Furthermore, this method can be adapted to a range of metapopulation structures (patch models and single populations). In the framework of this method, dispersal is only considered to be local, and it is assumed that the mixing effects of dispersal cancel out at a regional scale (Melbourne and Chesson 2006).

Our study focuses on population growth rather than individual growth. While scale transition theory can also be extended to describe the difference between individual fitness and landscape fitness, we do not focus on this aspect here but see Melbourne and Chesson (2006) for how this term can be calculated using field data.

Several studies have empirically estimated a scale transition term and have found that landscape population growth tends to be slower than expected from estimates of local population growth (Melbourne and Chesson 2005, 2006, Benedetti-Cecchi et al. 2012, Holt and Chesson 2016). However, studies to date have only examined small-scale, stable systems and none have included the spatial effects of dispersal (Melbourne and Chesson 2005, 2006, Englund and Leonardsson 2008, Benedetti-Cecchi et al. 2012, Holt and Chesson 2016). We address this knowledge gap by examining scale transition terms for a large scale, rapidly expanding system over multiple sites using large-scale data obtained from remote sensing. This big-data approach opens up the possibility of using the scale-transition term approach to a much wider set of study systems for which temporal trends in spatial patterns can be rapidly quantified (Gurevitch et al. 2016). Finally, we choose to model an issue of acute conservation importance where realistic estimates of population growth are essential to prioritise management actions. If mean field estimates prove unreliable predictors of future population growth then they may undermine effective action.

We examine the invasion of conifers, as they are rapidly spreading species and an issue for many countries in the Southern Hemisphere (Higgins and Richardson 1998, Richardson and Rejmánek 2004, Essl et al. 2011). There is evidence that density affects the spread of conifer invasions through both facilitation and competition (Richardson and Bond 1991, Nuñez et al. 2009, Dovčiak et al. 2014, Hayward et al. 2015, Sapsford et al. 2020); therefore we would expect that spatial processes have a large influence on population growth. In this system (as in many others), there is a disconnect between the spatial scale of invasions and the available ecological data. Individual invasions can cover areas over 10 km^2, but often population parameters and invasion dynamics are measured in small plots (Carrillo-Gavilán and Vilà 2010, Tomiolo et al. 2016) or short transects (Langdon et al. 2010, Nuñez and Paritsis 2018). However, we have previously used remote sensing to quantify the

spatial distribution (but not age structure) of conifer invasions at several sites across large spatial scales and multiple years (Sprague et al. 2019).

By combining remote sensing imagery data, captured over multiple time periods and sites, with estimates of changes in population size, we compare the reliability of mean field and scale transition term estimates of population growth for a dynamic system at broad spatial scales for the first time. The questions this study aims to answer are as follows:

1) How large are the spatial variation of density and density dependence components of the scale transition term?
2) How important is a scale transition term compared to the mean field estimate, and what are the consequences of ignoring the spatial effects of density on population growth?
3) How consistent is the scale transition term across multiple landscapes and years?

Material and methods

To scale up population growth estimates and determine the effect of spatial processes on estimates of population growth, we gathered data from eight large-scale alien pine invasion sites over multiple time steps. The average area of the study sites was 3.0 km^2, with the smallest being 0.24 km^2 and the largest over 16 km^2 (Table 1). Time steps were dictated by the availability of aerial and satellite images for each of the sites. These imagery data have been collected every 2–3 years for the past decade, giving us 1–2 time periods per site. With these data, we divided the sites into one hectare-sized grid-cells and then used these data to estimate the difference between the local and landscape estimates of population growth.

Remote sensing imagery and data processing

We gathered imagery from eight invasion sites across the South Island of New Zealand (Fig. 1) for multiple time steps (2–4 points in time) using a combination of high resolution aerial imagery gathered from the Land Information New Zealand (LINZ) archives and high resolution satellite imagery downloaded from Google Earth. We selected sites in grasslands, where imagery was available from multiple time steps, separated by at least two years and have sub-meter spatial resolution to accurately detect trees. We considered only sites where it was possible to distinguish intentionally planted areas of trees and any managed areas where trees were cut down or sprayed with herbicide. This way we could determine the invasions' likely seed source and whether the invasions had been modified by management.

The spatial resolution for each site was approximately 0.5 m and the spectral resolution was three bands (red, green and blue) for a natural colour image. Georeferencing and imagery specifications are summarised in the Supporting information. To detect the pine trees, we used an unsupervised, pixel-based classification method. First, we thresholded the imagery to separate out the dark-coloured trees against the light-coloured background vegetation (Ke and Quackenbush 2011). Then we segmented the pixels identified as trees using a process called watershedding in order to delineate the tree canopies (Komura et al. 2004, Wang et al. 2004, Deng et al. 2016). We extracted the centre point of each polygon identified as a tree, and for each site and time step, we generated a file of the point locations of every tree detected.

We verified the accuracy of our image classification procedure with field surveys at one site (Sprague et al. 2019), and more details can be found in the Supporting information. All image classification was conducted in R using the following

Table 1. Mean density and variance of densities for each site and time-step. The extents of the sites expand over time, showing that the populations were spreading. However, the population models in this study only examined the infilling of the populations and excluded any long-distance dispersal. Note that LINZ refers to the agency Land Information New Zealand.

Site	Imagery source	Year imagery captured	Site extent (km^2)	Mean no. of trees per ha	Variance in no. of trees per ha	Coefficient of variation
Ohau	Google Earth	2011	5.15	17	541	137%
Ohau	LINZ	2014	5.94	65	8554	142%
Mt Barker	Google Earth	2010	4.84	212	13 070	54%
Mt Barker	LINZ	2016	6.02	412	58 726	59%
S. Pukaki	Google Earth	2006	2.33	64	5066	111%
S. Pukaki	LINZ	2008	2.54	134	18 411	101%
S. Pukaki	LINZ	2014	2.89	235	58 341	103%
S. Pukaki	Google Earth	2016	3.30	319	121 670	109%
Shelterbelt W.	LINZ	2006	0.24	155	22 269	96%
Shelterbelt W.	Google Earth	2010	0.37	196	23 463	78%
Shelterbelt E.	LINZ	2008	0.42	141	25 655	114%
Shelterbelt E.	Google Earth	2010	0.60	264	73 232	103%
Shelterbelt E.	LINZ	2014	0.73	355	72 678	76%
Quailburn	LINZ	2008	1.41	211	53 667	110%
Quailburn	LINZ	2014	1.70	388	65 350	66%
Ohau Village	LINZ	2006	1.28	109	25 152	145%
Ohau Village	Google Earth	2011	1.43	298	66 700	87%
Irishman Creek	LINZ	2008	11.20	40	12 209	276%
Irishman Creek	LINZ	2014	16.60	105	21 888	141%

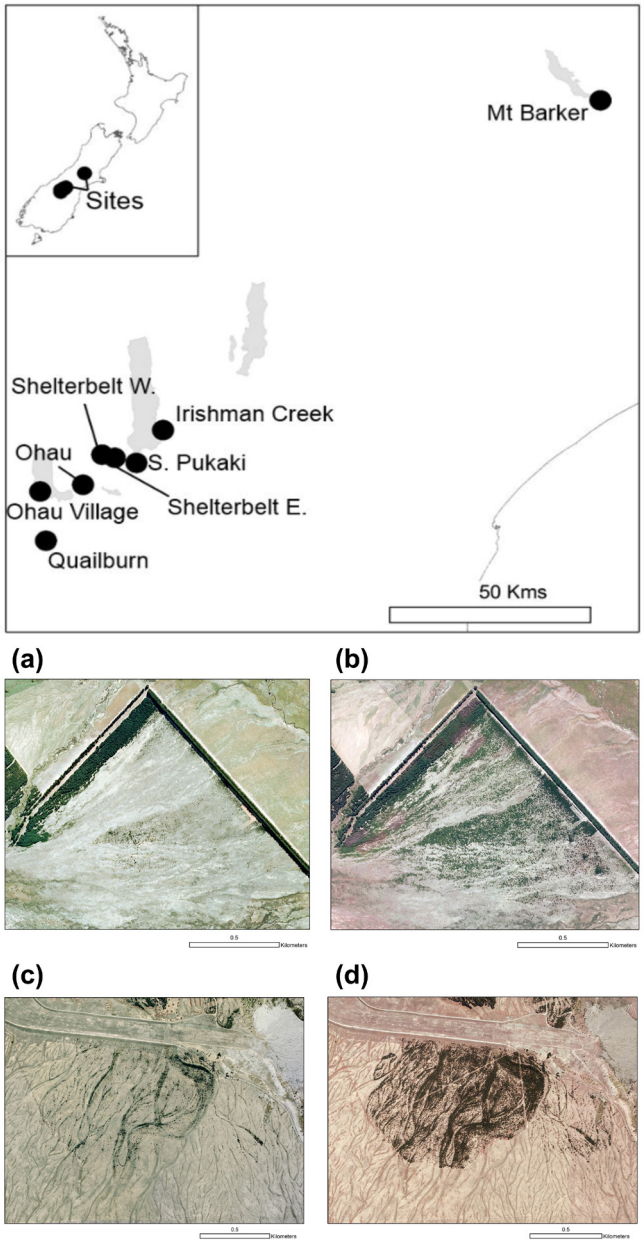

Figure 1. The map shows the locations of the eight sites as indicated by the black points. All of the sites were located in the Canterbury province on the South Island of New Zealand. Prominent lakes in the region are included on the map in grey as areas of reference. The following imagery photos are included in the figure to illustrate the variation in densities across sites and time: (a) Quailburn site in 2008 (imagery provided by Land Information New Zealand); (b) Quailburn site in 2014 (imagery provided by Land Information New Zealand); (c) S. Pukaki site in 2008 (imagery provided by Land Information New Zealand); (d) S. Pukaki site in 2014 (imagery provided by Land Information New Zealand).

packages: EBImage (Pau et al. 2010), rgdal (Bivand et al. 2014), raster (Hijmans et al. 2020) and sp (Pebesma and Bivand 2005) (<www.r-project.org>).

To prepare the data derived from the image classification and detection methods for use in our population growth models, we first divided each site into a set of one hectare grid-cells, and counted the number of trees in each cell for each time step. We used one hectare as the cell size because previous work suggests that most seeds will disperse less than 200 m (i.e. within a single hectare grid-cell or to the adjacent grid-cells) (Buckley et al. 2005, Caplat et al. 2012a, Wyse et al. 2019). we removed the grid-cells with no trees in them in the first time step. Thus we decided to examine only the population growth process known as infilling. Infilling can be defined as when the spreading population colonises areas within its existing range, and it occurs because of local dispersal (Warren et al. 2013, Taylor et al. 2015). We did not gather local demographic data such as birth and death rates at a smaller spatial scale and therefore did not examine directly local demographic dynamics.

Population growth models

Let $N_{t,i}$ denote the population density in a single cell i = 1, …, I at time t. The population growth can then be modelled using the Gompertz model, which has been frequently used to estimate negative density dependence of populations (Thorson et al. 2015, Roy et al. 2016), as follows:

$$\log\left(N_{t+1,i}\right) = F_{\text{Gompertz}}\left(N_{t,i}\right)$$

where

$$F_{\text{Gompertz}}\left(N_{t,i}\right) = a_t + b_t \log\left(N_{t,i}\right) + \varepsilon_{t,i}$$

where the intercept represents the density-independent growth (a) and the slope represents the density-dependent growth (b). Note, that the parameters a and b are time-step specific.

A value of b greater than 1 represents faster than exponential growth, a value of $b = 1$ exponential growth, a value of b less than but close to 1 ($0.75 \leq b < 1$) represents weak density dependence, and a value of b close to 0 ($0 > b \geq 0.25$) represents strong density dependence (Thorson et al. 2015).

To account for spatial autocorrelation due to dispersal at short to intermediate distances (< 200 m) and correlated environmental conditions in adjacent areas, we modelled the residual $\varepsilon_{t,i}$ as a spatial random effect for each time t via a conditional autoregressive (CAR) model (Besag et al. 1991) as follows:

$$\varepsilon_{t,i} \sim N\left(\overline{\varepsilon}_{t,-i}, m_t \tau_t\right)$$

where $\overline{\varepsilon}_{t,-i}$ is the average of the residuals (spatial random effects) over cells adjacent to the cell i, m_t is the number of these adjacent cells and τ_t is the spatial precision (i.e. inverse variance parameter). The adjacency relationship is encoded via a binary matrix W of dimensions $I \times I$, where $w_{i,j} = 1$ if the locations i and j are adjacent, and is 0 otherwise, i.e. all the adjacent cells are assigned equal weights. Adjacency was

defined as a cell being next-to or diagonal (i.e. eight adjacent cells); a location cannot be adjacent to itself.

The CAR model accounted for spatial autocorrelation by local smoothing, thereby mitigating neighbourhood effects of trees, and assumed the datasets to be isotropic (i.e. cells would disperse equally into their surrounding cells and there was no directional dispersal). Dispersal was therefore included in the spatial autocorrelation term indirectly. For each site and set of time-steps examined, we defined a new adjacency matrix based on the occupied areas in the site.

We ran our population growth models in a Bayesian framework. We used the following informative priors based on estimates of density dependence and density independent growth for similar Gompertz models in the literature (Dennis et al. 2006, Thorson et al. 2015):

$$a_t \sim N(0, 0.2)$$

$$b_t \sim N(0, 1)$$

where $N(m,w)$ refers to a Gaussian (normal) distribution with mean m and precision w. Note that the second parameter in the normal priors is precision (inverse variance) rather than standard deviation. The precision parameter of the CAR prior, τ, was given a gamma prior

$$\tau \sim G(0.1, 0.1)$$

where $G(a,b)$ refers to a Gamma distribution with the shape and scale parameters a and b respectively. The posterior summaries were not sensitive to the priors, and all posterior distributions converged.

We set up and ran a model for each time period (i.e. a pair t and $t+1$) and site. Time periods were the difference between time t and $t+1$, or $t+1$ and $t+2$ if there were three time observations for one site. Time observations were not regular due to the availability of imagery data. The models were fitted with Markov chain Monte Carlo (MCMC) sampling, implemented in the R package Nimble (de Valpine et al. 2017). The package uses BUGS language to encode the model and the code may be found in the Supporting information.

To check for the statistical effect of spatial autocorrelation, we compared our CAR model to the non-spatial model, where the residuals were modelled as:

$$\varepsilon_{t,i} \sim N(0, \tau_t)$$

To compare the spatial and non-spatial models, we calculated the Watanabe–Akaike information criterion (WAIC) value (Watanabe 2010).

Each model used three chains and ran for 10 000 iterations with the first 5000 samples discarded as the burn-in. More details about the setup for running and assessing convergence of the models is in the Supporting information. In the Supporting information, we also show example goodness of fit plots for three sites to illustrate how the model predictions compared to the observed values.

All of the models were coded and run in R (<www.r-project.org>).

Estimating a scale transition term

Before we estimated the strength of the scale transition term, the variation in density and density dependence were estimated for each site and time period. We compared the coefficients of variation for each site and time step to determine the relative amount of variation in tree densities.

We adapted the work of Chesson et al. (2005) to examine the scaling of population growth across landscapes. Landscape population growth rate can be approximated as the growth rate calculated using the mean field plus a transition term called a scale transition term representing $F(N)$ approximated by a second-order Taylor series expansion.

At a landscape scale, the population growth will be the function for population growth at a local scale averaged across a region plus a transition term (a scale transition term):

$$\underbrace{\overline{F(N)}}_{\substack{\text{Projected population}\\ \text{at time } t+1}} = \underbrace{F(\overline{N_t})}_{\substack{\text{Mean field}\\ \text{approximation}}} + \underbrace{\frac{1}{2}\text{Var}(N_t)F''(\overline{N_t})}_{\text{Scale Transition Term}}$$

The density within each grid-cell at time t is represented by N_t, and the average density of all grid-cells across a site at time t is represented by $\overline{N_t}$. The predicted population density averaged across all cells at time $t+1$ is $\overline{F(N)}$, and the mean field approximation of population growth averaged across all cells at time t is represented by $F(\overline{N_t})$. The function $F(N)$ maps N_t to N_{t+1} using the Gompertz equation in Eq. 1. Equation 4 is a general statement, and since we are using the Gompertz equation to explain population growth, our results in this paper are particular to this equation. As seen in Eq. 4, the scale transition term depends on the variance in tree densities at the start of the observation period (var(N)) and the nonlinear growth of the site's population ($F''(N)$). To calculate the variance in densities across a site, we used the population level formula for variance among all grid-cells in a given site. In this calculation we excluded grid-cells with a tree density of 0, since these were ignored in our population model of infilling growth.

To calculate the nonlinear growth component of the scale transition term, $F''(N)$, we took the second derivative of the Gompertz population growth equation with respect to population density (see the Supporting information for more details). Because the nonlinear growth term needed the estimates of the density independent growth and density dependence, we used the distributions for these parameters estimated from our population growth model to calculate

$F''(N)$ for each site and time period. We used the 95% central (equal tailed) credible intervals of the estimates of the scale transition terms to determine whether the estimates were above/below zero for each site examined.

Results

Sites and models

The number of trees detected at the sites at the first time step ranged from approximately 3500 for the smallest site (Shelterbelt West) to over 200 000 trees for the largest site (Mt Barker). The aerial imagery data tended to be higher resolution than the satellite imagery (Supporting information), but this did not affect our ability to detect mid to large-sized trees (over 2.5 m canopy diameter).

We ran models at eight sites, and in three sites it was possible to model two or more time periods, leading to 11 models in total. In each case the spatial versions of the models (i.e. those with autocorrelation in the residuals) better fit the data than the non-spatial versions (WAIC values in the Supporting information). Thus, the parameter estimates from the spatial models were used for every site and time period. Additionally, all parameter estimates converged, and the goodness of fit plots showed that the model accurately predicted the observed values (Supporting information).

Variation in density and estimates of density dependence

We found that tree density did vary greatly across the study landscapes as shown by the coefficients of variation which were often above 100% (Table 1). The variation in density was not necessarily consistent for each site either, with some sites having similar coefficients of variation between time periods (i.e. Ohau, S. Pukaki and Mt Barker) and others having different coefficients of variation (i.e. Quailburn, Ohau Village and Irishman Creek).

Density independent growth parameters were consistently large, which was expected for these rapidly growing populations (Fig. 2a). There was some variation among sites, but most had a density independent growth parameter of around 2. This implies that over that time period, for one tree in a grid-cell in time t, there were approximately six trees in time $t+1$. Density dependence was negative in all sites and time periods, such that at higher densities growth rates were lower (Fig. 2b). For most sites, density dependence was weak to moderate in strength ($0.5 < b < 1$), although for the Quailburn density dependence was strong ($b < 0.25$). When running our model diagnostics, we found that our estimates of density independent growth and density dependence were correlated. When the intrinsic growth rate was high, there was high density dependence as well. Since the data have not been centred, estimates for intercept and slope have a tendency to be correlated as an artefact of the regression model.

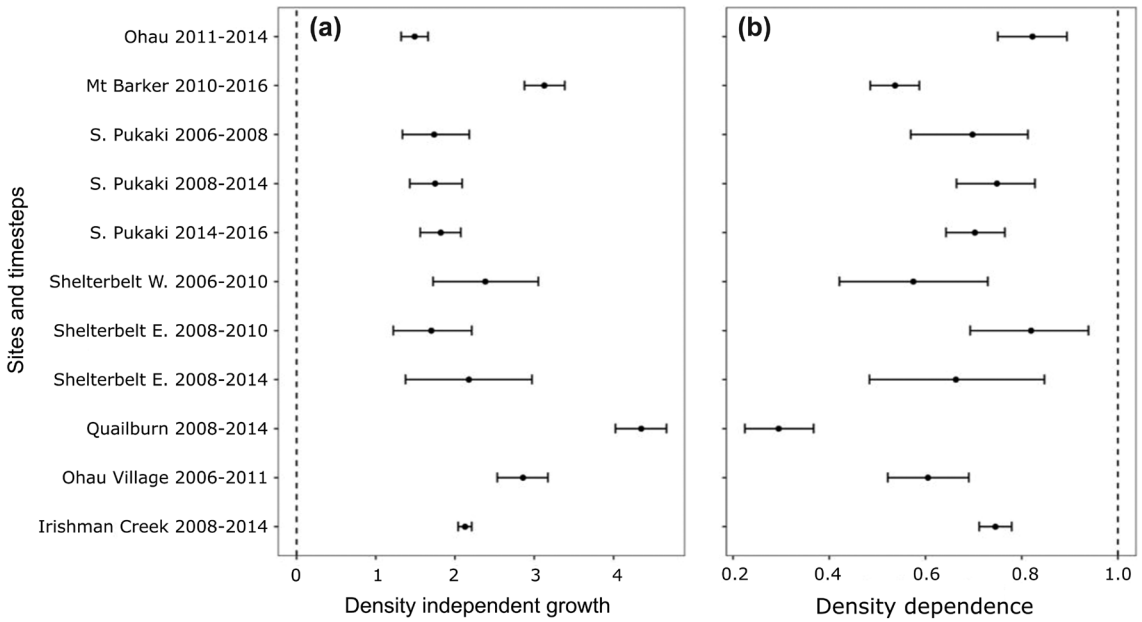

Figure 2. (a) Estimates of density independent growth were high for all sites examined. These density independent growth values are the a parameter posterior means from the model, and error bars are 95% credible intervals. (b) Most site and time periods had weak to moderate degrees of density dependence. These density dependence values are the b parameter posterior means from our model, and error bars are 95% credible intervals.

Estimates of the scale transition term

The estimates of a scale transition term for all sites were negative, indicating that growth at the landscape scale is slower than would be expected from the mean field estimate. All of the 95% credible intervals indicated that the posterior probabilities of the estimates were below zero (Fig. 3a). For sites where we had multiple time periods, the scale transition terms became stronger (more negative) over time. For a site such as Irishman Creek with an STT of −95, there would be an average of 95 fewer trees per cell per time period than expected if population growth was estimated using the average density of trees across a landscape. For most sites, there would be an average of between 10 and 50 fewer trees per cell per time period. Since the time periods varied for each site depending on when the imagery was available, we did not directly compare the magnitude of the scale transition terms between sites. All of the estimates of the scale transition term were significantly negative, and this means that spatial processes slow population growth.

When we expressed the scale transition terms as a proportion of the mean field estimates, we found that the scale transition terms were typically only 10–25% the size of the mean field estimates (Fig. 3b). This means that if the effects of spatial variation were ignored and the mean field estimate was used, estimates of population growth would be inflated by around 5–35% for most sites. The only exception of these values was one site and time period (Irishman Creek 2008–2014) when the scale transition term was almost 75% of the mean field estimate. This means that for this site, the expected population growth when spatial effects are ignored would be over-estimated by approximately four times.

Discussion

This study is the first to estimate the scale transition term for multiple sites and time periods and for populations that are rapidly changing in size. We compared the effect of adding a scale transition term when estimating population growth. In our system we found that estimates of the scale transition term were typically large and always significantly different from 0. At each site, population growth was negatively density dependent. As a result, estimates of the scale transition term were also negative indicating slower landscape scale growth than would be expected under a mean field model. We found that there was large spatial variation of density across our sites, and this variation contributed greatly to the scale transition term.

We found that density independent growth was positive and high across all sites. These estimates were expected given that we already suspected that the growth of these conifer invasions was quite high (Buckley et al. 2005, Caplat et al. 2012b). Density dependence was negative and varied in magnitude between sites. Few other studies have estimated density dependence in expanding tree populations; however, our estimates of density dependence were consistent when comparing them to other forest systems (Brook and Bradshaw 2006, Johnson et al. 2012a, Zhu et al. 2015).

Our estimates of the scale transition term were large and negative, thereby showing the consistent effect of spatial processes across dynamic invasions. The STT was strongly influenced by variation in tree densities at the start of our observation period which was many orders of magnitude larger than the non-linearity in population growth (Supporting information). This scenario may be common in rapid invasions where interactions/competition among individuals are relatively weak, but population densities vary enormously from one location to another. These estimates were similar to those found in previous studies (Melbourne and Chesson 2006, Benedetti-Cecchi et al. 2012), although these studies did not examine non-stable, expanding populations as ours did. Our results imply that the mean field estimates of population growth over-estimate landscape population growth. When scaling up population growth data from a local to a landscape scale, we should use the mean field approach with caution unless we can be certain that there is a random distribution of individuals across an area (Law et al. 2000). This is because the mean field approximation averages non-linear functions, leading to inaccuracies in estimates of population growth. Instead, to properly scale up data, we will need to account for spatial processes because of the variance of density and individual growth responses to density. The importance of these spatial processes for population growth has been acknowledged before (Levin 1992, Dieckmann et al. 2000, Chave 2013); however, to date, they have not been applied at such a large spatial scale or over such a long time series. Thus, accounting for these processes will now need to become part of the general practices of broad-scale ecology.

Our methods provide one way forward for future studies examining population growth across spatial scales. Instead of using experimental data to parameterise our population growth models, high resolution aerial and satellite imagery enabled us to capture population density data over time, for multiple sites, and at a broad spatial scale. The scale transition terms were estimated using a Taylor series truncated at the second order, which allowed us to simplify the estimation of population growth while still keeping the accuracy of the results (Barabás et al. 2018, Ellner et al. 2019). The Bayesian population growth models allowed us to account for the spatial autocorrelation between one hectare grid-cells. Since we required flexible methods to model population growth, we used the Gompertz model, which was easily adapted to include autocorrelation terms (Thibaut and Connolly 2020). Biologically, the Gompertz is a preferred approach for large datasets such as ours because it can be considered a first order approximation of more complex models of density dependence (Dennis and Taper 1994, Ives et al. 2003, Brook and Bradshaw 2006, Thibaut and Connolly 2020). Nevertheless our goodness of fit tests in the Supporting information suggest that the Gompertz model does a reasonable job of capturing information about population growth.

Our model offers a straightforward representation of dispersal by including dispersal in the spatial autocorrelation

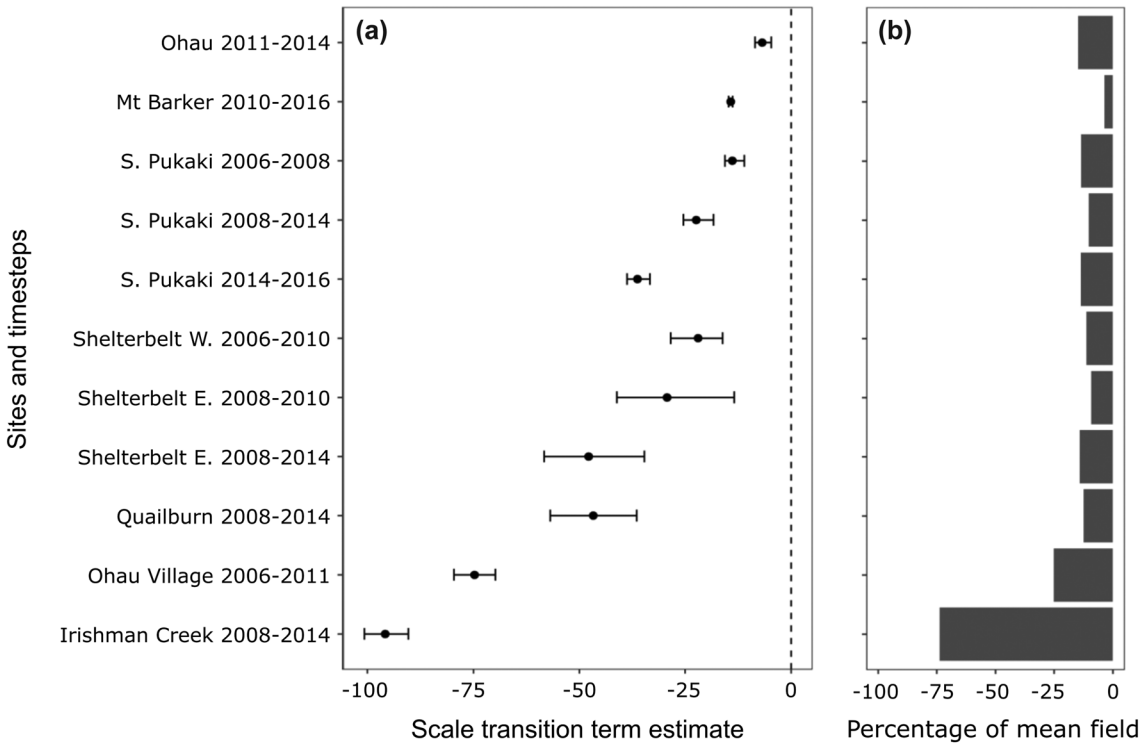

Figure 3. Estimates of scale transition terms. To interpret the scale transition terms, a positive scale transition term indicates that projected population growth is greater than indicated by the mean field approximation. A negative scale transition term indicates that projected population growth is less than indicated by the mean field approximation. For this study, a scale transition term estimate of −1 would mean that there was one fewer tree per grid-cell per time period than expected if population growth was estimated using the mean field estimate. (a) All estimates of the scale transition term were negative and significantly different from 0. Error bars are 95% credible intervals. (b) The magnitude of each scale transition term expressed as the percentage of the scale transition term of the mean field estimate of population growth (i.e. scale transition term/mean field estimate).

term, enabling future studies to examine dynamic systems as well. Other studies estimating a scale transition term have accounted for dispersal at a local scale but they have assumed that dispersal outside of a plot or grid-cell is not relevant at landscape scales (Melbourne and Chesson 2006, Benedetti-Cecchi et al. 2012). Because we are studying a rapidly expanding system and dispersal is the key process of that expansion, we suspect that dispersal is relevant at landscape scales for dynamic systems (Loreau et al. 2003, Meynard et al. 2013). Combining these methods with the scale transition term approach (adapted from Chesson et al. 2005, Chesson 2012), we were able to effectively compare population growth estimates between small (one hectare) and large (> 1 km^2) spatial scales. Other studies seeking to study population growth at the broad scale should consider using these methods.

This study was not without its limitations. We only estimated density dependence at the scale of the grid-cells (100 × 100 m). Other results may be possible using smaller grid cells because positive and negative density dependence in conifer invasions has been found to act at different scales (Dovčiak et al. 2014). Furthermore, we did not gather local demographic data or examine changes in the age structure of conifers over time, and we limited the study to only examining short-term dynamics. Additionally, the scale transition terms were estimated using variance in densities and density dependence, which limited our ability to explore potential sources of heterogeneity in density and population growth. It is quite possible that the importance of density dependence will vary with life-stage e.g. where seedlings and saplings experience greater density dependent effects than large adults. From a management perspective however, a focus on the adult age class is likely sufficient as the main target is the reproductive individuals since they are responsible for the current spread. Furthermore, the adult reproductive life stage inherently captures the results of density dependent growth from previous life stages (Harte 2011).

In this study, we assumed that dispersal was equal in all directions and additionally dispersal was only implicitly included in the spatial autocorrelation term. In the future it would be desirable to include a more mechanistic model of dispersal to explore the possibility of directional dispersal (Caplat et al. 2012a). A final limitation of our study is that we only examined infilling population growth, which is when a population spreads into areas within its existing range (Warren et al. 2013, Taylor et al. 2015), and therefore we did not examine long distance dispersal. Infilling is important and understudied (Johnson et al. 2012b), but our approach offers fewer insights about long distance dispersal, another

key stage in conifer invasions, and therefore limits the application of this study to the management of infilling or the reduction of density in an invasion. However, where possible, management objectives often aim for the eradication of invasive conifer trees from an area, which effectively is reducing the density of conifer trees at a site.

For the management of these invasions, our findings indicate that current predictions of population growth could be too high (Ministry of Primary Industries 2014), and the outlook of growth due to infilling is perhaps not as bleak as predicted. Additionally, the population growth parameters estimated for each site can help with projections of population growth. For future research on introduced conifers, this study also illustrates an appropriate scale to study conifer invasions. By accounting for dispersal and environmental heterogeneity at one-hectare sized grid-cells, we were able to estimate meaningful population growth parameters for these invasions.

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Author contributions

Rowan Sprague: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Funding acquisition (equal); Investigation (equal); Methodology (lead); Project administration (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Philip E. Hulme**: Conceptualization (equal); Formal analysis (supporting); Funding acquisition (supporting); Investigation (supporting); Methodology (supporting); Supervision (supporting); Validation (supporting); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (equal). **Elena Moltchanova**: Conceptualization (supporting); Formal analysis (supporting); Investigation (supporting); Methodology (supporting); Validation (supporting); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (equal). **William Godsoe**: Conceptualization (equal); Formal analysis (supporting); Funding acquisition (supporting); Investigation (equal); Methodology (supporting); Supervision (lead); Validation (equal); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (equal).

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Data availability

The data is available on the Dryad Digital Repository <https://doi.org/10.5061/dryad.wstqjq2mm> (Sprague et al. 2021).

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